

Functional anatomy of *Fossula fossiculifera* (D'Orbigny, 1843) (Bivalvia: Mycetopodidae)

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Abstract: *Fossula fossiculifera* (D'Orbigny, 1843) is the type species of the genus *Fossula*, a member of the family Mycetopodidae. The genus is restricted to South America. The species is found in the Paraná River and its tributaries from Argentina to the state of São Paulo, Brazil, and in the Paraguaçu River on the Atlantic ridge of the state of Bahia, Brazil. These medium-sized bivalve molluscs live buried in muddy substrata. The incumbent aperture is fringed along the inner fold while the excurrent aperture is smooth. The ctenidia are of type D (Atkins, 1937a). The stomach is a type IV structure (Purchon, 1958) with morphological differences on the right wall. The posterior gut is voluminous; the typhlosole runs throughout its length. The animals are hermaphrodites and incubate their eggs in the marsupium of the inner demibranchs.

In South America the family Mycetopodidae is represented by six genera: *Fossula*, *Iheringella*, *Monocondylaea*, *Leila*, *Anodontites*, and *Mycetopoda* (Parodiz and Bonetto, 1963). According to Ortmann (1921), *F. fossiculifera* (D'Orbigny, 1843) occurs in the Paraná River and its tributaries from Argentina to the state of São Paulo, Brazil. Bonetto (1961), when discussing the geographic distribution of unionoideans in the Argentine Republic, extended the distribution of *F. fossiculifera* to the Paraguaçu River, on the Atlantic ridge of the state of Bahia, Brazil.

Hass (1930) recognized three subspecies of *Fossula*: *F. fossiculifera fossiculifera*, *F. fossiculifera balzani* (Ihering, 1893), and *F. fossiculifera braziliensis* (Ihering, 1910). According to this author, *F. fossiculifera fossiculifera* is distributed as described by Ortmann (1921), whereas *F. fossiculifera balzani* occurs in the Paraguai River, state of Mato Grosso do Sul, Brazil, and *F. Fossiculifera braziliensis* occurs in the Paraguaçu River, state of Bahia, Brazil. Ortmann (1921) and Bonetto (1961) recorded a single species for the genus. Lange de Morretes (1949) reported two species, *F. fossiculifera* and *F. braziliensis*, without mentioning the species reported by Hass (1930).

In the present report, I shall follow the systematic treatment proposed by Bonetto (1961). Systematic studies on the functional anatomy of limnic bivalves in Brazil, include those conducted by Mansur (1972, 1973), Hebling and Penteado (1974), Hebling (1976), Veitenheimer and Mansur (1978), Mansur and Anflor (1981), Mansur and Silva (1990) and Avelar and Santos (1991). Additional studies of the functional anatomy of the Mycetopodidae

have been reported by Hebling (1976), who studied the comparative anatomy of *Anodontites trapesialis* (Lamarck, 1819) and *A. trapezeus* (Spix, 1827). Mansur (1974) examined the shell and the morphology of the digestive system of *Monocondylaea minuana* (D'Orbigny, 1835). Mansur and Silva (1990) studied the comparative morphology and microanatomy of *Bartlettia stefanensis* (Moricand, 1856) and *A. tenebricosus* (Lea, 1834). Veitenheimer and Mansur (1978) studied the morphology, histology and ecology of *Mycetopoda legumen* (Ortmann, 1888).

The objective of the present investigation was to study the structure, ciliary feeding currents and other functional adaptations of *Fossula fossiculifera* as a contribution to the understanding of the biology of the species, and also to provide the basis for future research related to South American unionideans.

MATERIALS AND METHODS

Live specimens of *Fossula fossiculifera* specimens were collected from the Pardo River, municipality of Ribeirão Preto (21° 7'S, 47° 45'W). Five specimens were captured at three-month intervals (15 Feb, 15 May, 17 Aug and 21 Nov). A total of 20 animals were kept alive in the laboratory in aquaria at 25°C. Some animals were anesthetized with magnesium chloride and fixed in 10% buffered formalin for 24 hr. Others were preserved in 70% alcohol for morphological examination.

To complete the anatomical studies, detailed drawings of the animals, and of the arrangements of their internal organs, were performed using anesthetized ani-

mals. Ciliary currents of the mantle, ctenidia, labial palps and stomach were observed under a stereomicroscope using carmine or carborundum as indicators. Some structures (palps, ctenidia, mantle and visceral mass) were fixed in aqueous Bouin's, cut into 7-10 μm sections, and stained with Ehrlich's hematoxylin and eosin, for anatomical examination.

HABITAT

According to Bonetto (1961), *Fossula fossiculifera* occurs in the Paraguai River and in the middle and upper Paraná River, reaching the Atlantic coast of the state of Bahia in the Paraguaçu river. The animals preferentially live buried in muddy substrata under calm waters and can be captured at depths of 0.7 to 1.0 m. The bivalves burrow almost completely into the substratum, leaving only their posterior end exposed (Fig. 1). They can be captured by probing the river bottom with one's hands or feet. Several species of bivalve were captured at the collection site, among them *Anodontites trapesialis*, *Diplodon rotundus gratus* (Wagner, 1827), *D. fontaineanus* (D'Orbigny, 1835), *D. delodontus expansus* (Küster, 1856), *D. martensis* (Ihering, 1892), and *Castalia undosa undosa* (Martens,

1827). The most abundant species were *D. rotundus gratus* and *A. trapesialis*, followed by *D. fontaineanus* and *F. fossiculifera*, with the rare occurrence of *D. delodontus expansus* and *D. martensis*.

It should be pointed out that bivalves of the families Hyriidae or Mycetopodidae, except *Anodontites trapesialis*, that occur in the Pardo River measuring less than 2 cm in length are difficult to identify because the juvenile shells are very similar and all characterized by the presence of six to 12 ribs in the umbonal region.

FUNCTIONAL MORPHOLOGY

SHELL. The shell of *Fossula fossiculifera* (Figs. 2 and 3) is subcircular in contour, equivalve and inequilateral, with a winged posterior border rising above the umbo. The periostracum in species smaller than 2.0 cm is yellowish to olive-brown in color in specimens ranging in size from 2.0 to 7.0 cm in length. In specimens larger than 7.0 cm, the periostracum is brownish green. These observations are similar to those reported by Ihering (1910) and Ortmann (1921).

The umbo (u) is prosogyrate, with a worn periostracum. The lunule (lu) is small, dark in color and with oval contours. The outer opisthodetic ligament (l) starts below the umbo and extends posterodorsally to the valve isthmus. Two minor ribs originate in the umbo and extend to the ventral region, the most dorsal one ending in the region of the diaphragm that separates the apertures. In young and adult specimens, the growth lines anastomose, especially in the posterior region where they are elevated and have a lamellar aspect. The above observations are sim-

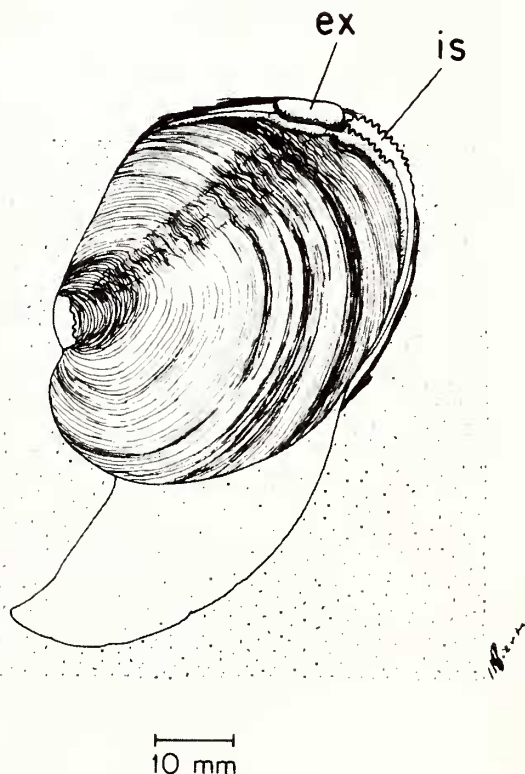


Fig. 1. *Fossula fossiculifera*. External view of the left side showing extended foot and aperture (ex, excurrent aperture; is, incurrent aperture).

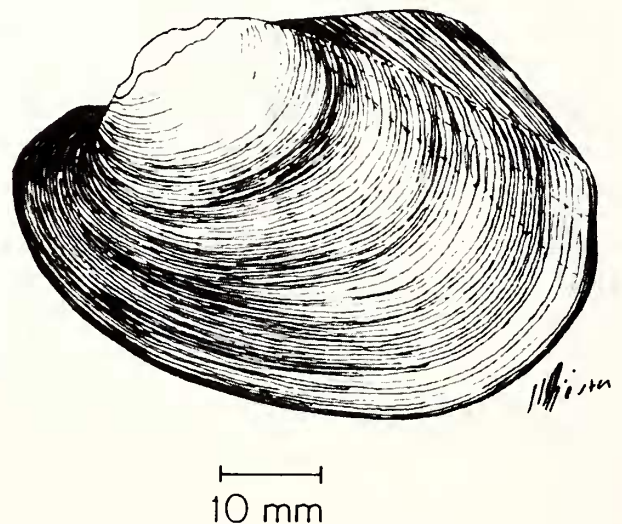


Fig. 2. *Fossula fossiculifera*. External view of the left valve showing the lines of growth.

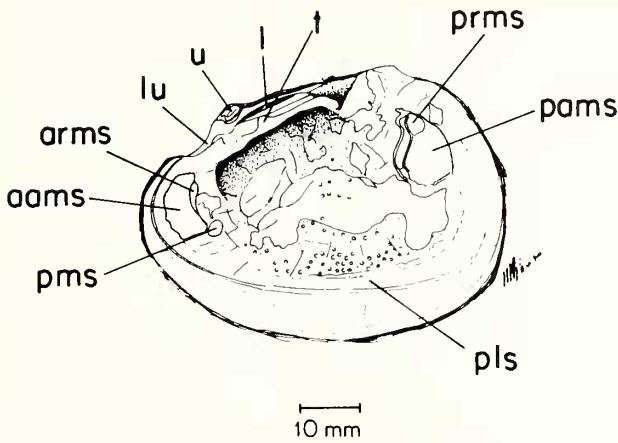


Fig. 3. *Fossula fossiculifera*. Internal view of the right valve, showing the muscle scar (aams, anterior adductor muscle scar; arms, anterior retractor muscle scar; l, ligament; lu, lunule; pams, protractor muscle scar; prms, posterior retractor muscle scar; t, tooth; u, umbo).

ilar to those reported by Hebling (1976) for *Anodontites trapezeus*. According to Ortmann (1921), the valve measurements of *Fossula fossiculifera* varied from 80 to 85%, in relation to length. In the present study, height was 76 to 84% of length in a lot of 20 animals.

The hinge is well developed, with one pseudocardinal tooth in the left valve and two pseudocardinal teeth in the right valve. In specimens larger than 7.0 cm, the spacing between the pseudocardinal teeth in the right and left valves becomes increasingly wider and the teeth simply become a projection of the hinge, eventually even becoming obsolete. The inner surface of the valve is white or bluish white, with the submarginal region yellowish cream in color. In recently sacrificed specimens with soft parts removed, the inner surface stains greenish in color. This results from pallial mucus that polymerizes when in contact with the external medium, and forms a thin film. After a few weeks, this film detaches from the shell revealing the white pearly color of the nacre.

The umbonal cavity is shallow and the scars of the dorsal mantle muscles were not observed. Hebling (1976) reported the presence of these muscles in *Anodontites trapezialis* and their absence in *A. trapezeus*. The scars of the anterior adductor muscle (aams) and of the anterior retractor muscle of the foot (arms) (Fig. 3) are continuous and present an oval contour. The anterior retractor muscle of the foot forms a deep scar in a position dorsal to the anterior adductor muscle. The scar of the protractor muscle of the foot (pms) has a rounded contour and is located in the region of the posterolateral third of the anterior adductor muscle. The scar of the posterior retractor muscle of the foot (prms) is narrow and dorsally located in relation to the

scar of the posterior adductor muscle. The scar of the posterior adductor muscle (prms) is approximately of the same size and shape as that of the anterior adductor muscle. In specimens measuring 40 and 80 mm in length, the size of the scars reached six and 12 mm, respectively.

The pallial line (pls) starts below the scar of the anterior adductor muscle and continues parallel to the margin of the shell, ending at the base of the posterior adductor muscle scar. The margin of the mantle leaves a well defined scar that starts dorsally to the anterior adductor muscle and runs along the entire margin of the shell parallel to the scar of the pallial line and ending dorsally in the shell isthmus.

MANTLE. When the valve and mantle are removed from the left side of the animals, the pallial cavity is exposed. The outer (secretory) and median (sensory) folds of the mantle are quite close to each other. In the region of the incurrent aperture, the inner fold (muscular) has a fringed border appearing to be formed by small papillae, as defined by Ortmann (1921), that extend far forward, decreasing in size and gradually disappearing.

Posterior to the foot, approximately 1 cm dorsad from the shell margin, the mantle presents a muscular elevation forming an evagination that I term the posterior fold of the mantle (pfm) (Fig. 4 and elsewhere) and which ends at the point where the ctenidia join the mantle. Anterior to this fold, the mantle is not thickened, as shown in figure 5.

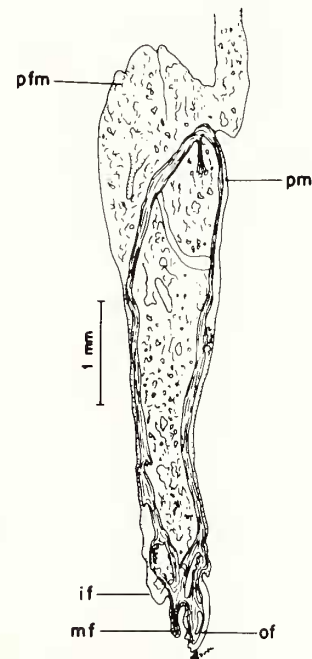


Fig. 4. *Fossula fossiculifera*. Frontal section of the posterior region of the edge of mantle showing the posterior fold of mantle and the pallial muscle on the mantle lobes (if, inner fold; mf, middle fold; of, outer fold; pm, pallial muscle; pfm, posterior fold of mantle).

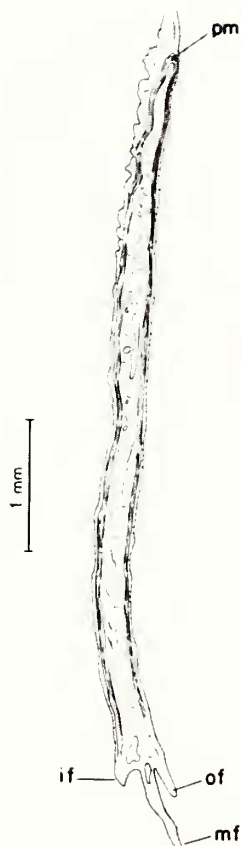


Fig. 5. *Fossula fossiculifera*. Frontal section of the anterior region of the edge of mantle and the pallial muscle (if, inner fold; mf, middle fold; of, outer fold; pm, pallial muscle).

The mantle margin on both the left and right sides presents two joining regions located dorsoventrally to the anal opening, defining the excurrent aperture. The incurrent aperture is characterized by the presence of fringes of the inner margin of the mantle. The mantle is yellowish in color, and the color of the inner, middle and outer lobes tends to be salmon. Between the inner and middle lobes, in the posterior region, there is black pigmentation that delimits the incurrent and excurrent apertures. The pedal opening is wide and starts in the region located posteroventrally to the anterior adductor muscle and is limited in the posterior region by the ventral region of the incurrent aperture, where the first fringes of the inner margin of the mantle arise.

APERTURES. The apertures of *Fossula fossiculifera* (Fig. 6) are of the A II type (Yonge, 1957). The excurrent aperture corresponds to the anal opening as defined by Ortmann (1921). It is wide with a smooth free border and becomes crenulated depending on the state of contraction. In living animals, the length of the excurrent aperture does not exceed 1 cm beyond the shell margin. The inhalant aperture

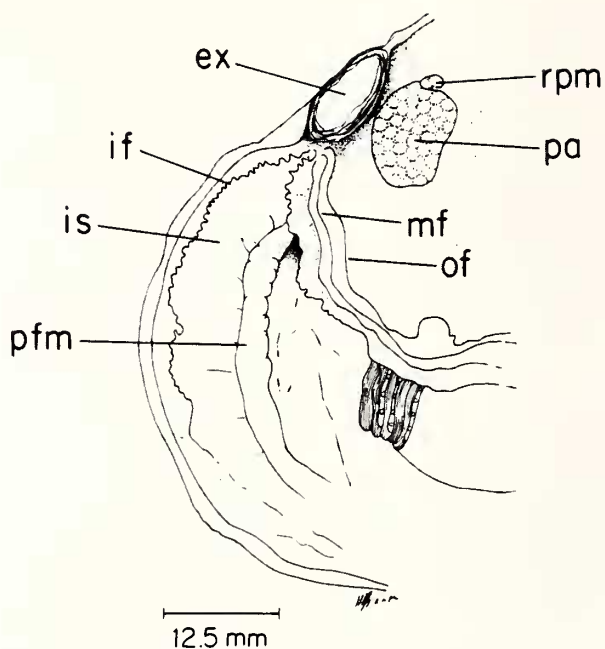


Fig. 6. *Fossula fossiculifera*. Frontal view of incurrent and excurrent apertures showing the posterior fold of mantle (ex, excurrent aperture; if, inner fold; is, incurrent aperture; mf, middle fold; of, outer fold; pa, posterior adductor; pfm, posterior fold of mantle; rpm, retractor posterior muscle).

is separated from the inner lobes of the mantle by a solid connection. The incurrent aperture has a fringed margin, and forms a continuous structure with the pedal opening. The length of the extended incurrent aperture does not exceed 1 cm from the shell margin in living animals buried in the substratum.

MUSCLE AND FOOT. The musculature of *Fossula fossiculifera* (Fig. 7) is similar to that of members of Hyriidae

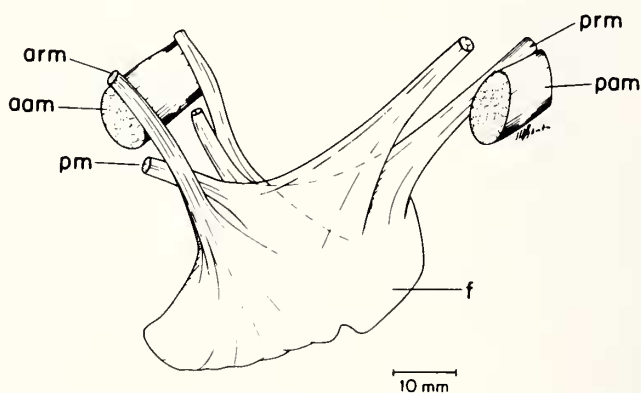


Fig. 7. *Fossula fossiculifera*. Lateral view of musculature after removal of the valves, mantle, palps and visceral mass (aam, anterior adductor muscle; arm, anterior retractor muscle; pam, posterior adductor muscle; pm, protractor muscle; prm, posterior retractor muscle).

and Mycetopodidae described by Mansur (1972), Hebling and Penteado (1974), Hebling (1976), and Avelar and Santos (1991). *Diplodon rotundus gratus*, *Anodontites trapesialis*, *A. trapezeus*, *Castalia undosa undosa* and *F. fossiculifera* all lack ciliation on the foot.

MANTLE CAVITY

Topography. The position of the main organs of the mantle cavity is indicated in figure 8. The visceral mass is yellow and a heavily ciliated region is responsible for rejectory currents that carry particles to the posterior region of the animal. The foot is salmon colored. The ctenidia are yellowish in color and extend posteriorly from the umbonal region to the base of the exhalant aperture. The mantle margins are free, leaving a wide pedal opening. The labial palps (lp) which are large and suboval in shape. The ventral margins of the labial palps are plain and without "sculpture".

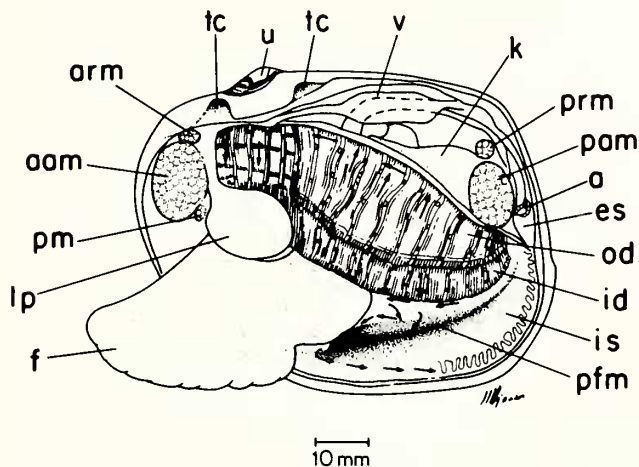


Fig. 8. *Fossula fossiculifera*. Organs and ciliary currents of mantle cavity after removal of left shell valve and mantle lobe (a, anus; aam, anterior adductor muscle; arm, anterior retractor muscle; ex, excurrent aperture; f, foot; id, inner demibranch; is, incurrent aperture; k, kidney; lp, labial palps; od, outer demibranch; pam, posterior adductor muscle; pfm, posterior fold mantle; pm, protractor muscle; prm, posterior retractor muscle; tc, pseudocardinal tooth; u, umbo; v, ventricle).

Labial Palps. The palps of *Fossula fossiculifera* (Figs. 9 and 10) are yellowish in color and symmetrical, with folded inner surfaces and smooth outer surfaces. An area with no folds exists on the inner surfaces of both the anterior and posterior region. The anterior region is connected to the proximal oral groove (pog) and the posterior region to the anterior channel (ac). The food particles that reach the labial palps arrive from the marginal food groove (g) of the inner demibranch, either from the anterior channel that directs particles from the outer demibranchs, or from the

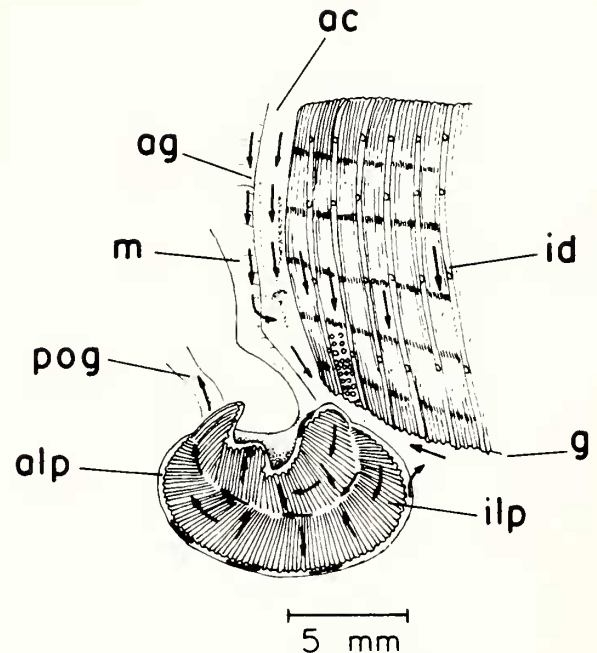


Fig. 9. *Fossula fossiculifera*. Labial palps of left side; arrows show direction of ciliary currents (ac, anterior channel; ag, anterior groove of mantle; g, food groove of inner demibranch; ilp, inner labial palps; m, mantle; olp, outer labial palps; pog, proximal oral groove).

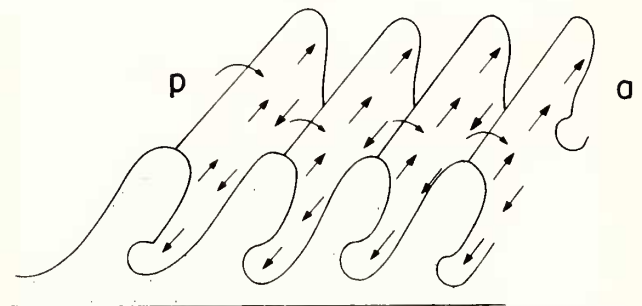


Fig. 10. *Fossula fossiculifera*. Diagrammatic representation of the ciliary mechanisms on the folded inner surface of the labial palps to show the various ciliary tracts (a, anterior; p, posterior).

anterior mantle groove (ag) that sends the particles from the mantle to the dorsum of the outer labial palps. This last path was observed by Mansur (1972) and Avelar and Santos (1991) in some Hyriidae. The mechanisms of particle screening and acceptance on the part of the labial palps are similar to those observed by Hebling (1976) and Avelar and Santos (1991).

Ctenidia. The ctenidia of *Fossula fossiculifera* are of type D (Atkins, 1937a), i.e. characterized by the presence of a marginal food groove along the inner demibranchs only. According to Atkins (1937a), this type of ctenidium is char-

acteristic of the Unionidae except *Etheria*.

The ctenidia of *Fossula fossiculifera* are arranged diagonally in relation to the visceral mass. The anterior filaments of the outer demibranchs are smaller than those of the inner demibranch and gradually increase in width posteriorly. The inner demibranch (id, Fig. 8) has approximately six more folds than the outer demibranch, which are clearly visible in the anterior region. The inner demibranch (Fig. 9) grows anteriorly in relation to the mantle and visceral mass, forming a wide and easily visible anterior channel (ac) that ends in the dorsal region of labial palps. The demibranchs (Fig. 11) are plicate, with filaments varying in number from 17 to 29 in the ascending lamella (alod) and descending lamella (dlod) of the outer demibranch (od). In the inner demibranch (id), the number of filaments in both lamellae (dlid and dlod) is the same as in the outer demibranch.

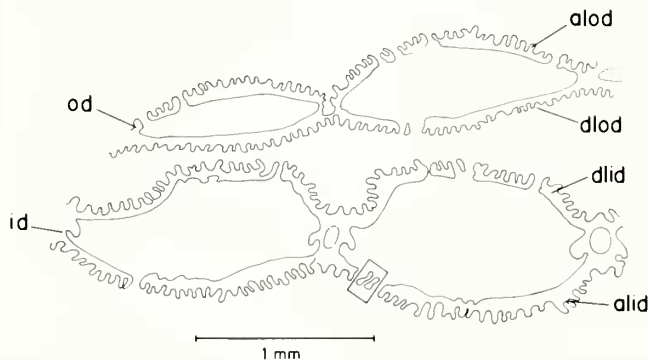


Fig. 11. *Fossula fossiculifera*. Transverse sections through a portion of outer and inner demibranchs showing arrangement of folds and filaments (alid, ascending lamella of inner demibranch; alod, ascending lamella of outer demibranch; dlid, descending lamella of inner demibranch; dlod, descending lamella of outer demibranch; id, inner demibranch; od, outer demibranch; square box outlines two frontal cilia enlarged in figure 12).

In living animals, the characteristic marsupium extends in the inner demibranch and is visible when the animal is brooding the eggs. The ctenidial ciliation of *Fossula fossiculifera* (Figs. 12 and 13) is similar to that of Hyriidae and Mycetopodidae studied by Hebling and Penteado (1974), Hebling (1976) and Avelar and Santos (1991). The frontal cilia (fc) and terminal cilia (tc) are approximately 6.1 μm and 10.4 μm long, respectively, in the inner demibranch. In the outer demibranch the frontal and terminal cilia are approximately 6.1 and 7.7 μm long, respectively. The laterofrontal cilia (lfc) are 18 μm long and the lateral cilia (lc) 14.6 μm long in both demibranchs.

The ciliary currents observed on the branchial surface are illustrated in figures 13 and 14. The screening mechanism of the type described for *Pinna* by Atkins (1937b) was also observed in *Fossula fossiculifera*, with

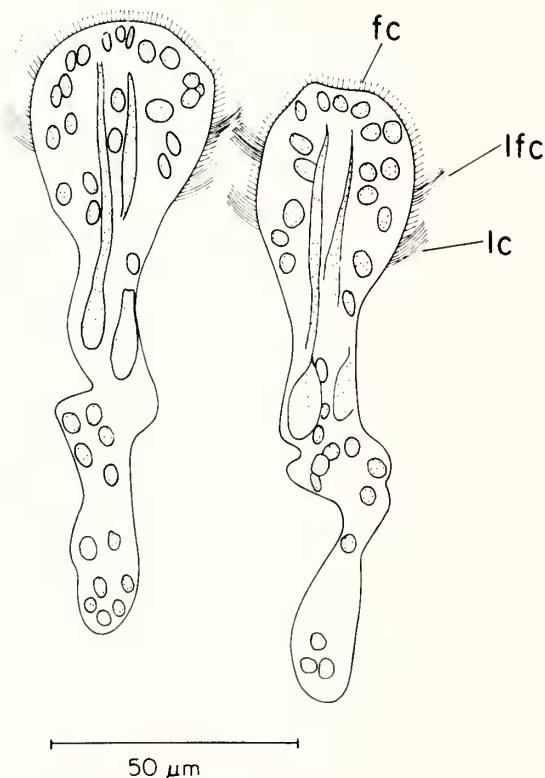


Fig. 12. *Fossula fossiculifera*. Transverse section of two filaments of inner demibranch to show cilia (fc, frontal cilia; lc, lateral cilia; lfc, laterofrontal cilia).

slight modifications (Fig. 15).

CILIARY CURRENTS OF THE MANTLE. The ciliary currents of the inner mantle surface are divided into two easily visible tracts (tracts 1 and 2) (Fig. 16). The particles that enter the pallial cavity via the incurrent aperture and contact the mantle in the region ventral to the posterior adductor muscle are selected according to weight and size. Small and light particles (tract 1) follow a posterior to anterior direction along a dorsal path between mantle and visceral mass. In the anterodorsal region, the particles follow a ventral direction and reach the outer surface of the outer palp where they are screened and are utilized or rejected. The heavy and/or larger particles (tract 2) are rejected in a dorsoventral direction. These particles reach the posterior muscle fold from where they are directed in a postero-anterior direction. Anterior to this fold, the current contacts the rejection current of the mantle (1), forming an anteroposterior rejection tract where particles move parallel to the free border of the mantle, forming a large rejection tract whose particles are eliminated at the base of the incurrent aperture. This screening mechanism is slightly different from that of Mycetopodidae (Hebling, 1976), Unionidae (Kellogg,

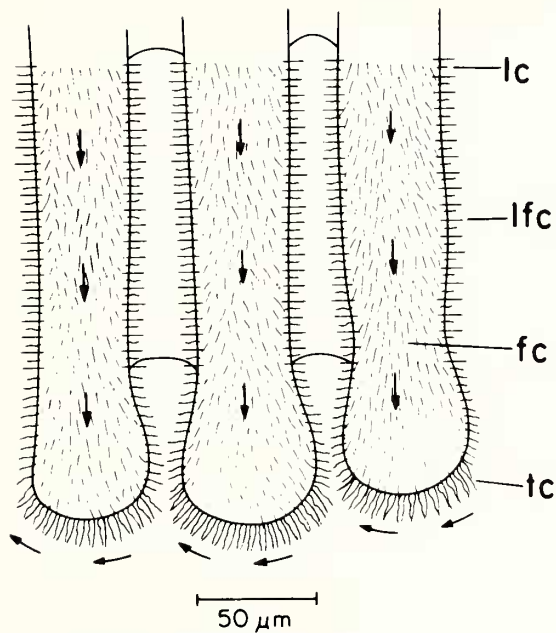


Fig. 13. *Fossula fossiculifera*. Cilia on outer surface of inner demibranch. Arrows indicate direction of ciliary currents, including the oral one (fc, frontal cilia; lc, lateral cilia; lfc, lateral frontal cilia).

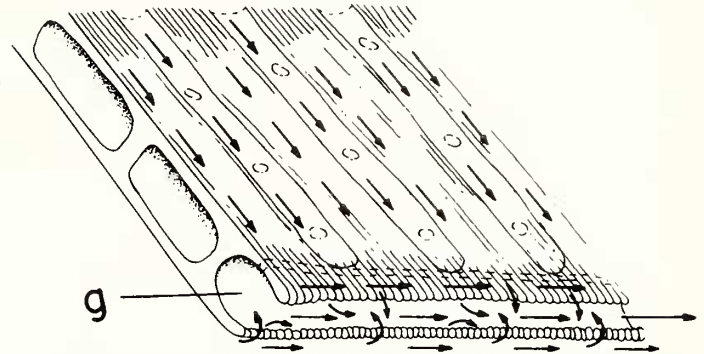


Fig. 15. *Fossula fossiculifera*. Diagrammatic view of edge of the inner demibranch showing the ciliary currents and the marginal groove. The arrows indicate direction of ciliary currents (g, marginal groove).

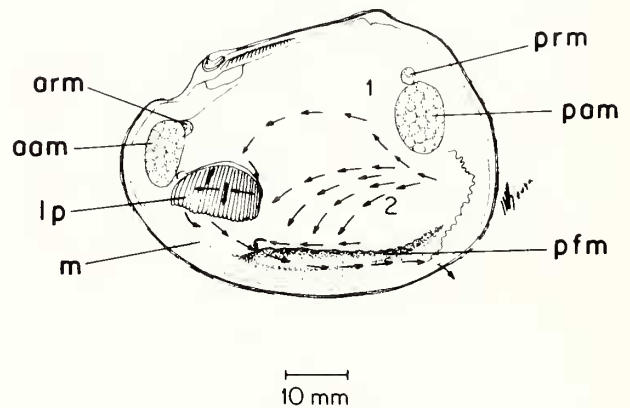


Fig. 16. *Fossula fossiculifera*. Inner surface of right mantle lobe showing ciliary cleansing currents (aam, anterior adductor muscle; arm, anterior retracter muscle; lp, labial palps; m, mantle; pam, posterior adductor muscle; pfm, posterior fold of mantle; prm, posterior retracter muscle; 1 and 2, ciliary tracts).

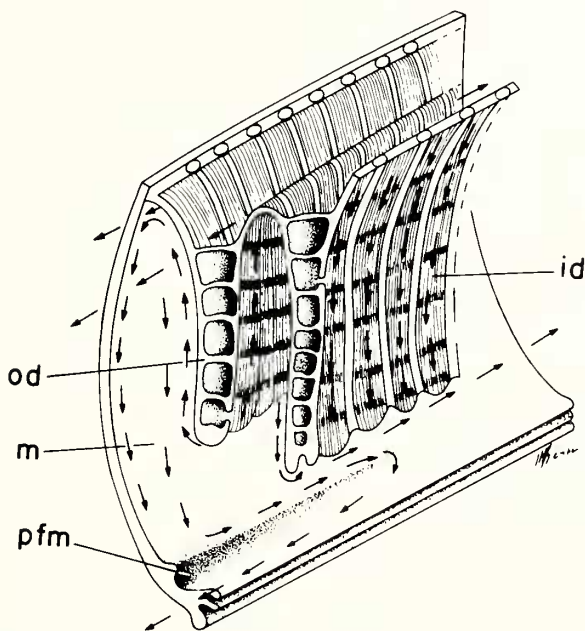


Fig. 14. *Fossula fossiculifera*. Diagrammatic view of mantle and ctenidia. The arrows show the direction of ciliary currents (id, inner demibranch; m, mantle; od, outer demibranch; pfm, posteiror fold of mantle).

1915), and Hyriidae (Hebling and Pentead, 1974; Avelar and Santos, 1991).

CILIARY CURRENTS IN THE VISCERAL MASS.

The ciliary currents in the dorsal region of the visceral mass run in a ventral direction. At the border between the visceral mass and the foot there is a rejectory tract that sends particles rejected by the labial palps and inner demibranch to the posterior region. The currents running in the ventral direction join those of the rejectory tracts and in this manner the rejected particles are sent toward the posterior end of the visceral mass where they fall in to the rejectory tract of the mantle. Similar rejectory tracts have been detected in the visceral mass of marine bivalves such as the Petricoliidae (Narchi, 1975) and freshwater bivalves such as Hyriidae (Avelar and Santos, 1991).

ALIMENTARY CANAL. The general topography of the digestive tract is illustrated in figure 17. The mouth (mo) is located in the posteroventral region of the anterior adductor

muscle. The mouth is followed by an esophagus (oe) whose inner wall has grooves and folds that are interrupted at the entrance to the stomach by a transverse ridge (rm) (Fig. 18). The stomach is located in the anterodorsal region of the visceral mass and is enveloped by the digestive diverticula. The stomach of *Fossula fossiculifera* is type IV (Purchon, 1958), as is also the case for Unionidae (Graham, 1949; Purchon, 1958; Dinamani, 1967; Kat, 1983a, b); Mycetopodidae (Hebling, 1976; Veitenheimer and Mansur, 1978; Mansur and Silva, 1990) and Hyriidae (Avelar and Santos, 1991). The general morphology of the stomach, the complexity of the ciliary currents and screening areas and the contiguous intestinal and crystalline style sac (ss) (Fig. 18) apertures are similar to those observed in the bivalve families noted above. However, it should be pointed out that *F. fossiculifera* has a configuration of the right wall of the stomach similar to that of *Bartlettia stefanensis* (Moricand, 1856) and *Anodontites tenebricosus* (Lea, 1834) described by Mansur and Silva (1990). There are three apertures on the right wall of the stomach, a large one in the posterior region, the posterior pouch (pp), that is located in a more ventral position and whose opening into the stomach is marked by the end of the tongue of the minor typhlosole (tm). This duct is adjacent to the screening area (sa3). The second aperture, the anterior pouch (ap), is located in a more dorsal position close to the opening of the esophagus. This aperture is connected to the dorsal hood by a screening area (sa8). The smaller aperture (ddd2) corresponds to the duct described by Purchon (1958) in *Anodonta cygnea*. The stomach configuration observed in *F. fossiculifera* differs from that of *A. cygnea* (Purchon,

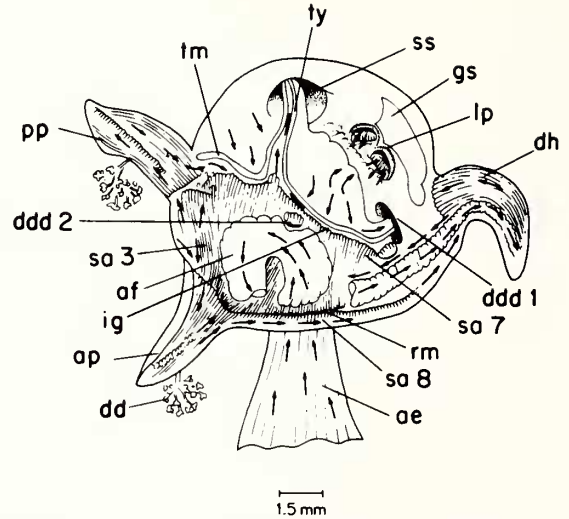


Fig. 18. *Fossula fossiculifera*. Structure of interior of stomach opened by a middorsal incision. Arrows show direction of ciliary current (ap, anterior pouch; dd, digestive diverticula; ddd-1, orifice of left duct of digestive diverticula; ddd-2, orifice of right duct of digestive diverticula; dh, dorsal hood; gs, gastric shield; ig, intestinal groove; lp, left pouch; oe, esophagus; pp, posterior pouch; rm, transverse ridge; sa-3, principal sorting area; sa-7, sorting area below esophageal orifice; sa-8, sorting area on anterior roof of stomach; ss, orifice of style and mid-gut; tm, minor typhlosole; ty, major typhlosole).

1958), *Lamellidens corrianus* (Dinamani, 1967), *A. trapezeus* and *A. trapesialis* (Hebling, 1976) and of the Unionidae described by Kat (1983a, b).

Two ducts are easily visible on the left wall (Fig. 18). According to Purchon (1958), these ducts are considered independent, the anterior one being the left pouch. The functioning of the stomach of *Fossula fossiculifera* recalls that of *Anodonta cygnea* (Graham, 1949; Purchon, 1958; Reid, 1965), *Anodontites trapezeus*, *A. trapesialis* (Hebling, 1976, and *Castalia undosa undosa* (Avelar and Santos, 1991). The intestine of *F. fossiculifera* is divided into three regions exactly as observed in *Acostaea rivoli* by Yonge (1978) and in *Anodontites tenebricosus* and *Bartlettia stefanensis* by Mansur and Silva (1990). The aperture of the style sac is associated with the first region, which extends from the opening of the stomach through a posterior loop of the intestine (Fig. 17, section 1). The second (section 2), consists of two loops of midgut rounded in section with a conspicuous typhlosole. The third (section 3) is an extensive loop terminating in the anus which represents an unusually capacious rectum occupying almost the entire width of the visceral mass and containing an even larger, more oval shaped, typhlosole.

PERICARDIUM, HEART, KIDNEY AND GONADS.

The pericardium, heart and kidney (Fig. 8) are similar to

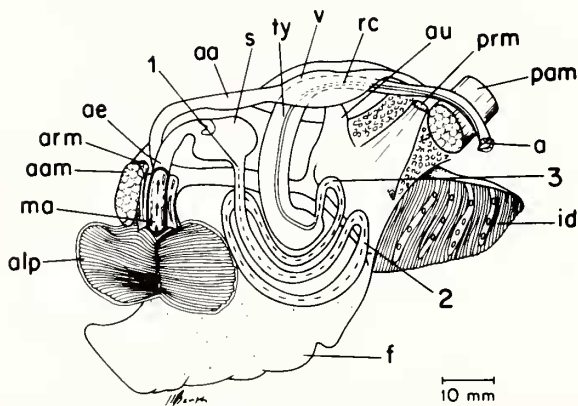


Fig. 17. *Fossula fossiculifera*. Alimentary canal seen from the left side. The numerals 1, 2 and 3 denote major subdivisions in the intestine posterior to the stomach (a, anus; aa, anterior aorta; aam, anterior adductor muscle; au, auricle; arm, anterior retractor muscle; f, foot; id, inner demi-branch; mo, mouth; oe, esophagus; olp, outer labial palps; pam, posterior adductor muscle; prm, posterior retractor muscle; rc, rectum; s, stomach; ty, typhlosole; v, ventricle).

those of *Anodonta* (White, 1942). *Fossula fossiculifera* is a hermaphrodite with male and female follicles present at a constant location in the visceral mass. Dissections and serial sections show that as spermatogenic tissue occupies the dorsal and posterior region of the gonad while the oogenic one occupies the ventral and anterior regions of gonad; these distribution is similar a *Anodonta imbecillis* (Kat, 1983c).

DISCUSSION

Studies of the functional anatomy of *Fossula fossiculifera* have revealed the existence of anatomical similarities among the Mycetopodidae, Hyriidae, Etheriidae and Unionidae studied by different investigators. *F. fossiculifera* lives in muddy substrata similar to those inhabited by *Diplodon rotundus gratus* studied by Hebling (1976) and *Castalia undosa undosa* described by Avelar and Santos (1991). In general, studies on freshwater bivalves have shown few special adaptations to a habitat of living close to the surface in relatively soft substrata and feeding on particles in suspension. This fact was also pointed out by Ansell (1961) for marine bivalves. The ability to burrow into soft substratum and occupy the same site for long periods of time, which is a characteristic of both *F. fossiculifera* as reported here, and *Anodontites trapezeus* as demonstrated by Hebling (1976), could be associated with the absence of the dorsal muscle or with the lack of functionality of the dorsal muscle, as observed in *A. trapesialis*, (Hebling, 1976) and *C. undosa undosa*, (Avelar and Santos, 1991).

Fossula fossiculifera has relatively simple papillae in the incurrent aperture. In a study on marine bivalves, Narchi (1972) attributed the simplicity of the siphons to the fact that the animals live in calm waters and feed on particles in suspension. Similarly, *F. fossiculifera* and other freshwater bivalves studied by Hebling (1976), Mansur (1973, 1974), Yonge (1978) and Avelar and Santos (1991) live in calm waters and feed on suspended particles.

The screening mechanism of the *Pinna* type observed in *Fossula fossiculifera* could contribute to more efficient particle selection and utilization. Indeed, when *F. fossiculifera* specimens were placed together with specimens of *Diplodon rotundus gratus*, *Castalia undosa undosa* and *A. trapesialis* in aquaria under the same conditions, survival time is higher for *F. fossiculifera*, perhaps due to the large amount of food accumulated in the hindgut of the animal. The ctenidia of *F. fossiculifera* are formed by more marked folds than those described by Mansur (1974) for *Monocondylaea minuana* and by Hebling (1976) for *A. trapezeus* and *A. trapesialis*.

A feature that seems to differentiate the Mycetopodidae from the Hyriidae is the arrangement of demi-

branchial folds. These are more conspicuous in the Mycetopodidae.

The ciliation observed in *Fossula fossiculifera* denotes the living habits of the animals, which prefer muddy environments with fine particles in suspension, such as silt clay and unicellular phytoplankton.

Another adaptation that can be attributed to a muddy type of environment is the marked development of the labial palps which, according to Yonge (1949) is common among animals burrowing in muddy substrata. According to Hebling (1976), the complexity of the ciliary currents in the palps leads to greater efficiency in particle selection. An additional adaptation observed in *Fossula fossiculifera* and perhaps related to more efficient particle selection could be related to the posterior fold of the mantle which overlaps at the point of entry of the incurrent aperture, joining the left side of the mantle to the right side and thus forming a functional canal preventing the flow of incurrent particles from meeting the flow of particles rejected by the mantle, visceral mass, palps and ctenidia. The latter are eliminated in the more ventral region of the incurrent aperture as pseudofeces. It appears that the posterior fold of the mantle also functions as a fourth fold also found in some Tellinoidea, apparently helping remove debris and pseudofeces from the mantle cavity (Yonge, 1948). The posterior mantle fold also occurs in *A. trapesialis*, a fact I have observed in specimens dissected in the laboratory, although Hebling (1976) did not mention its occurrence.

The stomach of *Fossula fossiculifera* and of most freshwater bivalves is type IV (Purchon, 1958), while some freshwater bivalve genera such as *Dreissena* and *Corbicula* have a type V stomach (Purchon, 1960). The stomach of *F. fossiculifera* and its complex ciliary current sorting areas have the same patterns as those of *Anodonta* described by Graham (1949), Purchon (1958) and Reid (1965). However, the stomach of *F. fossiculifera* differs from that of Unionidae and Hyriidae by presenting three apertures on the right wall, two of them large and one small. Hebling (1976) detected only a single digestive diverticulum duct on the right side in *A. trapezeus* and *A. trapesialis*. The stomachs of *F. fossiculifera* and of *Anodontites tenebricosus* and *Bartlettia stefanensis* described by Mansur and Silva (1990) are very similar, especially in terms of the right wall. The greater complexity of the stomach of *F. fossiculifera* could be related to greater efficiency in particle selection.

The general anatomy of the freshwater bivalves show only some differential features, but in the whole, the species are practically identical, furnishes no additional information useful for comprehension of the phylogeny of the genera, except some characters of the shell. Possibly, the posterior fold of the mantle, present in *Fossula fossiculifera* and observed in *Anodontites trapesialis* could

reveal a connection between the genera.

Studies performed with species of Mycetopodidae, Hyriidae and Unionidae, show that their similarity results from an adaptive convergence. In spite of being subjected to similar ecological factors, these species exhibit no differential morphological characters, but rather genetic ones (Hebling, 1976).

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LITERATURE CITED

- Ansell, A. D. 1961. The functional morphology of the British species of Veneracea (Eulamellibranchia). *Journal of the Marine Biological Association of the United Kingdom* 41:489-517.
- Atkins, D. 1937a. On the ciliary mechanism and interrelationships of lamellibranchs. Part III. Types of lamellibranchs gills and their food currents. *Quarterly Journal of Microscopical Science* 79:375-419.
- Atkins, D. 1937b. On the ciliary mechanism and interrelationship of lamellibranchs. Part II: Sorting devices on the gills. *Quarterly Journal of Microscopical Science* 79:339-373.
- Avelar, W. E. P. and S. C. D. Santos. 1991. Functional anatomy of *Castalia undosa undosa* (Martens, 1827) (Bivalvia, Hyriidae). *Veliger* 34:21-31.
- Bonetto, A. A. 1961. Acerca de la distribución geográfica de las nayades en la República Argentina. *Physis* 22:259-268.
- Dinamani, P. 1967. Variation in the stomach structure of the Bivalvia. *Malacologia* 5:225-268.
- Graham, A. 1949. The molluscan stomach. *Transactions of the Royal Society of Edinburgh* 61:737-778.
- Hass, F. 1930. Versuch einer kritischen sichtung der südamerikanischen najaden, hauptsächlich an hand der sammlung des Senckenberg-Museums. II. *Senckenbergiana* 12:30-52.
- Hebling, N. J. 1976. The functional morphology of *Anodontites trapezeus* (Spix) and *Anodontites trapesialis* (Lamarck) (Bivalvia, Mycetopodidae). *Boletim de Zoologia São Paulo*. 1:265-298.
- Hebling, N. J. and A. M. G. Penteado. 1974. Anatomia funcional de *Diplodon rotundus gratus* Wagner, 1827 (Mollusca, Bivalvia). *Revista Brasileira de Zoologia* 34:67-80.
- Ihering, H. Von. 1910. Über brasilianische najaden. *Abhandlungen Der Senckenbergischen Naturforschenden Gesellschaft*. 32:111-140.
- Kat, P. W. 1983a. Genetic and morphological divergence among nominal species of North American *Anodonta* (Bivalvia: Unionidae). *Malacologia* 23:361-374.
- Kat, P. W. 1983b. Morphologic divergence, genetics, and speciation among *Lampsilis* (Bivalvia: Unionidae). *Journal Molluscan Studies* 49:133-145.
- Kat, P. W. 1983c. Sexual selection and simultaneous hermaphroditism among the Unionidae (Bivalvia: Mollusca). *Journal of Zoology*, London 201:395-416.
- Kellogg, J. L. 1915. Ciliary mechanisms of lamellibranch with descriptions of anatomy. *Journal of Morphology* 26:625-701.
- Lange, De Morretes. F. 1949. Ensaio de catálogo dos moluscos do Brasil. *Arquivos do Museu Paranaense Curitiba*. 7:5-21.
- Mansur, M. C. D. 1972. Morfologia do sistema digestivo de *Castalia undosa martensi* (Ihering, 1891) (Bivalvia, Hyriidae). *Iheringia Zoologia* 41:25-34.
- Mansur, M. C. D. 1973. Morfologia do sistema digestivo das espécies do gênero *Diplodon* Spix, 1827 do rio Guafô Rio Grande do Sul (Unionacea - Hyriidae). *Iheringia Zoologia* 43:75-90.
- Mansur, M. C. D. 1974. *Monocondylaea minuana* Orbigny, 1835: Variabilidade da concha e morfologia do sistema digestivo (Bivalvia, Mycetopodidae). *Iheringia Zoologia* 45:3-25.
- Mansur, M. C. D. and L. M. Anflor. 1981. Diferenças morfológicas entre *Diplodon charruanus* Orbigny, 1835 e *D. pilsbryi* Marshall, 1928 (Bivalvia, Hyriidae). *Iheringia Zoologia* 60:101-116.
- Mansur, M. C. D. and M. G. O. Silva. 1990. Morfologia e microanatomia comparada de *Barlettia stefanensis* (Moricand, 1856) e *Anodontites tenebricosus* (Lea, 1834) (Bivalvia, Unionoidea, Muteloidea). *Amazoniana* 11:147-166.
- Narchi, W. 1972. Comparative study of the functional morphology of *Anomalocardia brasiliensis* (Gmelin, 1791) and *Tivela mactroides* (Born, 1778) (Bivalvia, Veneriidae). *Bulletin of Marine Science* 22:643-670.
- Narchi, W. 1975. Functional morphology of a new *Petricola* (Mollusca, Bivalvia) from the littoral of São Paulo, Brasil. *Proceedings of the Malacological Society of London* 41:451-465.
- Ortmann, A. E. 1921. South American naiades; a contribution to the knowledge of the fresh-water mussels of South America. *Memoirs of the Carnegie Museum* 8:451-670.
- Owen, G. 1953. On the biology of *Glossus humanus* (L) *Isocardia cor* Lam. *Journal of the Marine Biological Association of the United Kingdom* 32:85-106.
- Paradiz, J. J. and A. A. Bonetto. 1963. Taxonomy and zoogeographic relationships of the South American naiades (Pelecypoda: Unionacea and Mutelacea). *Malacologia* 1:179-213.
- Purchon, R. D. 1958. The stomach in the Eulamellibranchia; stomach type IV. *Proceedings of the Zoological Society of London* 131:487-525.
- Purchon, R. D. 1960. The stomach in the Eulamellibranchia; stomach type IV and V. *Proceedings of the Zoological Society of London* 153:431-438.
- Reid, R. G. B. 1965. The structure and function of the stomach in Bivalvia molluscs. *Journal of Zoology*, London 184:429-448.
- Simpson, C. T. 1914. A Descriptive Catalogue of the Naiades or Pearly Freshwater Mussels. Bryant Walker, Michigan. 1500 pp.
- Veitenheimer, I. L. and M. C. D. Mansur. 1978. Morfologia, histologia, e ecologia de *Mycetopoda legumen* (Martens, 1888) Bivalvia, Mycetopodidae. *Iheringia Zoologia* 52:33-71.
- White, K. M. 1942. Pericardial cavity and the pericardial gland of the Lamellibranchia. *Proceedings of the Malacological Society of London* 25:37-88.
- Yonge, C. M. 1949. On the structure and adaptation of the Tellinacea deposit feeding Eulamellibranchia. *Philosophical Transactions of the Royal Society of London* 234:29-76.
- Yonge, C. M. 1957. Mantle fusion in the Lamellibranchia. *Pubblicazioni della Stazione Zoologica di Napoli* 29:151-171.
- Yonge, C. M. 1978. On the monomyarian *Acostaea rivoli* and evolution in the family Etheriidae (Bivalvia, Unionacea). *Journal of Zoology*, London 184:429-448.

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